

On the occurrence of abnormal deciduous incisors during prenatal life in African “hystricomorphous” rodents

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Abstract

Examined early stages of dental development in four families and five genera of African “hystricomorphous” rodents. Small, abnormal, anterior deciduous incisors (dI1) were detected in both jaws, anterior to the large, normal dI2, in early developmental stages of all species examined: *Bathyergus janetta*, *Georychus capensis*, *Ctenodactylus gundi*, *Pedetes caffer*, and *Anomalurops beecrofti*. These small, abnormal teeth develop an irregular dentinal knot, but lack ameloblasts and enamel; a similar morphogenetic pattern occurs in the anterior deciduous incisors of sciurids and probably represents the ancestral condition in rodents. The functional significance of these abnormal teeth during ontogeny remains to be determined.

Introduction

Following the initial descriptions of abnormal or vestigial incisors in fetal and perinatal sciurids (FREUND 1892; ADLOFF 1898), murids (WOODWARD 1894), and castorids (HEINICK 1908), it remained unclear whether these rudimentary teeth, which develop anterior to the larger gliriform incisors, are restricted to a few groups of rodents, or whether they have a broader distribution within the order. Moreover, the occurrence of these abnormal teeth appears to be variable within muroid and caviomorph rodents, as judged by published reports of their presence or absence. The rudimentary incisors have been studied most extensively in sciurids (ADLOFF 1898; LUCKETT 1985), where they appear to be a consistent feature of the prenatal dentition. A limiting factor in evaluating the distribution and possible functional significance of abnormal incisors in Rodentia is the relative lack of developmental studies of the dentition for most families of the order (see LUCKETT 1985).

Morphogenetic analysis indicates that the small, abnormal incisors of rodents are homologous with the first deciduous incisors (dI1) of the primitive eutherian dentition, and that the large gliriform incisors of the fetus and adult are dI2 (LUCKETT 1985). The ontogenetic and phylogenetic significance of rudimentary deciduous incisors in rodents remains to be elucidated, but a greater knowledge of their distribution in rodent families should provide additional insight into their biological role. To date, there appear to have been no developmental studies of the dentition for any of the African “hystricomorphous” or hystricognathous rodents. We use the term “hystricomorphous” in a structural rather than taxonomic context, especially in light of the uncertainties surrounding the phylogenetic relationships of the hystricomorphous but sciurognathous families Anomaluridae, Pedetidae and Ctenodactylidae (WOOD 1985).

Studies are currently in progress on morphogenesis of the cranium in the hystricognathous family Bathyergidae (MAIER and SCHRENK 1987; SCHRENK in press) and in the “hystricomorphous” families Anomaluridae, Pedetidae and Ctenodactylidae (SCHRENK, in press). These investigations have also provided the opportunity to examine aspects of dental development in these same families. The present report will be limited to an analysis

of the incisive region in these taxa; a more detailed description of the entire dentition will be presented elsewhere (LUCKETT, in prep.).

Material and methods

Most of the fetuses examined during the present study were borrowed from the embryology collection of the Hubrecht Laboratory, Utrecht, the Netherlands, and from the Van der Horst Collection, Department of Zoology, University of the Witwatersrand, Johannesburg, South Africa (see Table 1). Fetal heads were doubly embedded in paraffin and celloidin, sectioned serially at 10–14 μ , and stained with Azan. Serial sections of both jaws were examined histologically, in order to identify all developing tooth germs, and to homologize them by their relationships with each other and with adjacent skeletal elements and other landmarks of the fetal head.

Results

The stages of eutherian and rodent dental morphogenesis were described and illustrated in a previous publication (LUCKETT 1985) and will not be repeated here. The Table presents a summary of the most significant features of deciduous incisor development for each of the specimens examined during the present study.

Table 1. Developmental aspects of deciduous incisors in the upper jaws of African rodents

Species	Fetal length	dI ¹	dI ²
<i>Bathyergus janetta</i> VDH Coll. Ba 1	13 mm CR	Moderate sized, abnormal, late bell, early dentin	Large, middle bell stage
<i>Bathyergus janetta</i> VDH Coll. Ba 2	21 mm CR	Moderate sized, abnormal dentinal cap	Very large, late bell, possible odontoblasts
<i>Georchus capensis</i> Hub. Lab. RO 436	30 mm CR	Small, abnormal dentinal knot	Huge tooth; thick dentin & enamel
<i>Bathyergus janetta</i> VDH Coll. Ba 3	48 mm CR	No trace	Huge tooth; thick dentin & enamel
<i>Ctenodactylus gundi</i> Hub. Lab. 208a	15.5 mm CR	Tiny, abnormal, thin dentinal cap	Large, early cap stage
<i>Ctenodactylus gundi</i> Hub. Lab. 213	22 mm CR	Tiny, abnormal, dentinal knot, partly fragmented	Large, middle bell stage
<i>Ctenodactylus gundi</i> Hub. Lab. 224a	32 mm CR	Tiny, abnormal, dentinal knot, partly resorbed	Large, late bell, moderately developed dentin
<i>Ctenodactylus gundi</i> Hub. Lab. 233	41 mm CR	Tiny, irregular dentinal knot, partly resorbed	Large; thick dentin, moderately developed enamel
<i>Pedetes caffer</i> Hub. Lab. RO 184	24 mm CR	Small, abnormal, late bell, thin dentinal arc	Moderately large, late bud-early cap stage
<i>Anomalurops beecrofti</i> P. Charles-Dominique Coll.	44 mm CR	Tiny, abnormal, dentinal cap, partly resorbed	Large tooth; thick dentin, moderately developed enamel

Family Bathyergidae

In the earliest stage of *Bathyergus* examined, a fetus of 13 mm crown-rump length (= CR), the large dI2 in both jaws are in the middle bell stage, with early differentiation of the stellate reticulum (Fig. 1). These teeth lie within the jaw stroma and are connected to the

oral epithelium by a short, slender dental lamina. The dental lamina disappears immediately distal to this tooth germ, so that there is no suggestion of dI3 in either jaw. Lying anterior (mesial) to the large dI2 is a smaller, moderate-sized, late bell dI1 in both jaws (Fig. 2). This tooth is more differentiated than dI2, in that it exhibits a distinct layer of

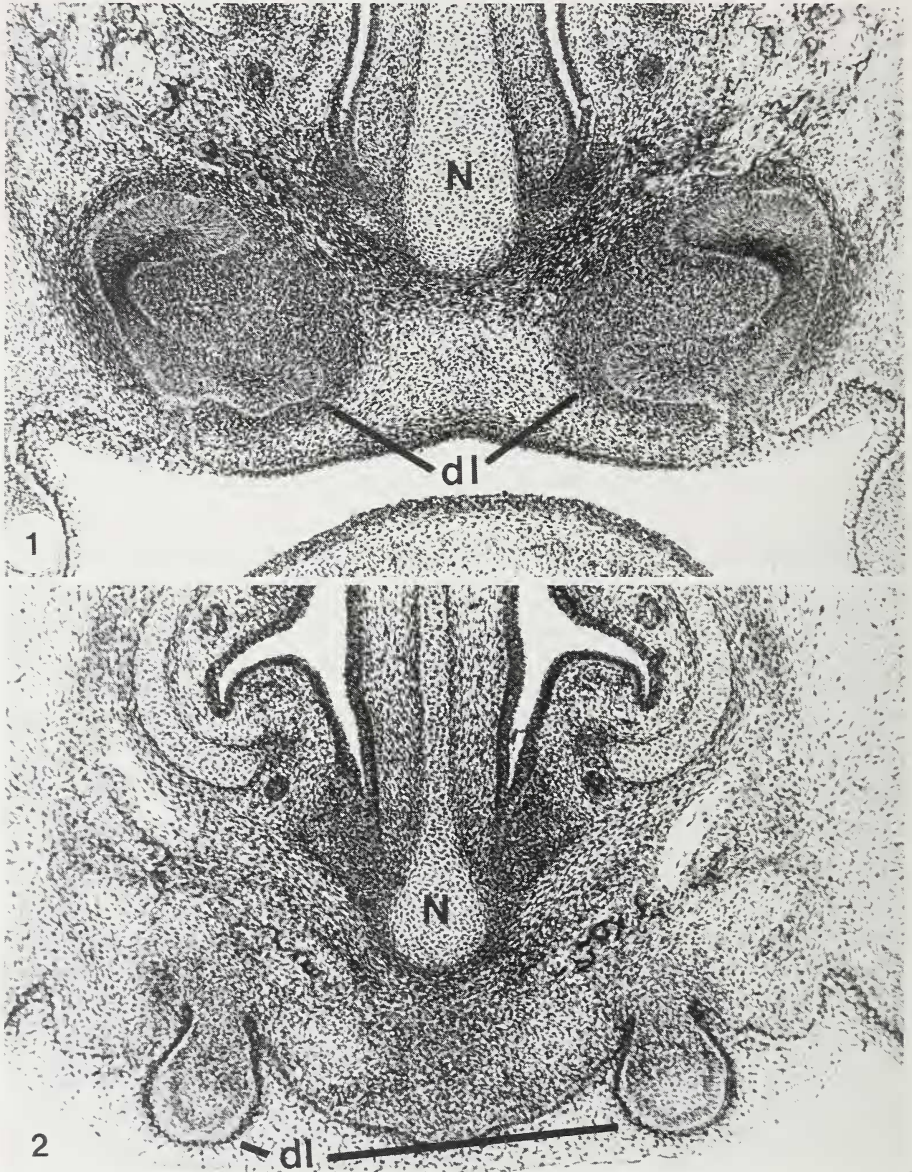


Fig. 1. *Batthyergus janetta* 13 mm CR fetus. Transverse section through upper jaw, showing the large, middle bell dI2 (dI), projecting into the jaw stroma, and overlain by the nasal septum (N). ($\times 250$). – Fig. 2. *Batthyergus janetta* 13 mm CR fetus. Transverse section through upper jaw, showing the small, abnormal bell stage dI1 (dI), projecting into the oral epithelium. Note the distinct, epithelioid layer of odontoblasts at the apex of the dental papilla. N = nasal septum. ($\times 250$)

odontoblasts and a thin layer of dentin or predentin. This anterior incisor is clearly abnormal, as indicated by its lack of stellate reticulum, and by the fact that it bulges into the overlying oral epithelium (Fig. 2). Consequently, the tooth germ retains a broad connection to the oral epithelium, so that a distinct dental lamina connection is not evident.

In a later fetus of 21 mm CR, the small to moderate-sized dI1 in both jaws consist of a densely cellular dental papilla overlain by a moderately developed dentinal cap, although a distinct layer of odontoblasts is lacking (Fig. 3). As in the previous stage, the abnormal tooth projects into the oral epithelium. There is no development of stellate reticulum, ameloblasts or enamel, and the outer and inner enamel epithelia are collapsed against each other, without differentiation. The more distal, greatly enlarged dI2 are in the late bell stage, with normal development of the stellate reticulum and an elongate dental lamina connection to the oral epithelium. Dentin has not yet formed on this tooth in the upper jaw, but a thin layer of dentin is developed on the lower dI2.

In a more mature 30 mm CR fetus of *Georychus capensis*, dI1 is represented only by a tiny, elongate, abnormal dentinal knot that projects into the oral epithelium of each jaw, and is connected to the underlying stroma by a slender connective tissue strand. This rudimentary tooth is closely followed by the enormous dI2, which possess thick dentin and thick enamel buccally in both jaws. In the latest stage examined, a 48 mm CR *Bathyergus* fetus, no trace of dI1 was found in either jaw (see Table 1).

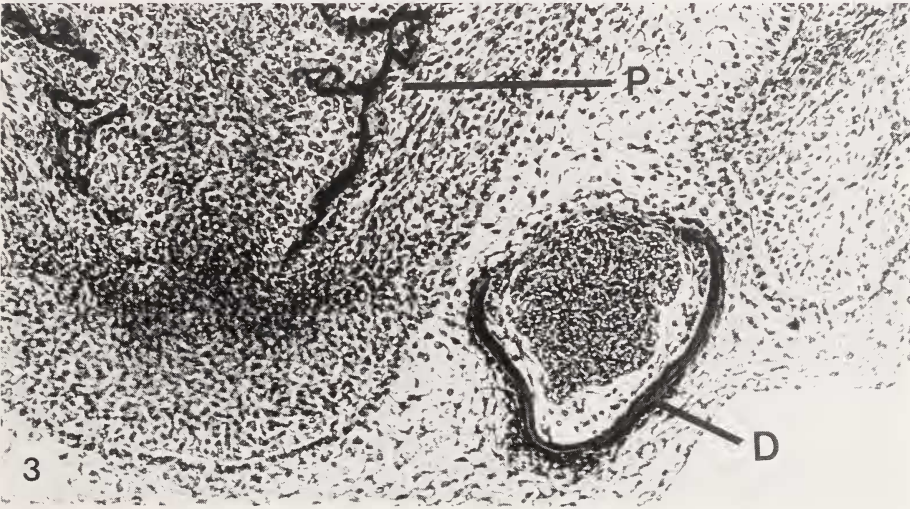


Fig. 3 *Bathyergus janetta* 21 mm CR fetus. Transverse section through upper jaw, showing the moderate-sized, abnormal dI1 projecting into the oral epithelium. A moderately-developed layer of dentin (D) is present, but there is no evidence of enamel, ameloblasts, or stellate reticulum. P = premaxillary bone trabeculae. ($\times 400$)

Family Ctenodactylidae

In a 15.5 mm CR fetus of *Ctenodactylus gundi*, a tiny nodular papilla, capped by a thin layer of dentin, projects into the basal surface of the oral epithelium in each jaw (see Table 1). As in *Bathyergus*, these abnormal dI1 lack stellate reticulum and a distinct separation between inner and outer enamel epithelia. The considerably larger dI2 are less differentiated, being in the early cap stage, but they exhibit normal relationships with the dental lamina and oral epithelium.

In later fetuses of 22, 32 and 41 mm CR, the tiny abnormal dI1 are represented by small dentinal knots, in which the irregular dentin exhibits varying degrees of fragmentation and partial resorption in both jaws (Fig. 4). In contrast, the large dI2 undergo normal differentiation of stellate reticulum, dentin and enamel during these stages (see Table 1).

Families Pedetidae and Anomaluridae

We have examined only a single fetus from each of these families to date (see Table 1), and we will describe them together. In a 24 mm CR fetus of *Pedetes caffer*, small, bell-shaped dI1 lie immediately beneath the oral epithelium and retain a broad connection to the latter. A thin layer of dentin covers the apex of the dental papilla, but odontoblasts are scattered within the dentin, rather than forming a distinct layer. The larger dI2 are less differentiated; they have only attained the late bud-early cap stage.

In a later fetus of *Anomaluroops beecrofti* (44 mm CR), dI1 in each jaw consists of a tiny, abnormal dentinal cap (Fig. 5), which is partially resorbed at its basal surface. These teeth lie at the anterior ends of the jaws, immediately beneath the oral epithelium. Distal to this tooth lies the large, normal dI2, with thick dentin and moderately developed enamel on its buccal surface.

Discussion

The findings of the present study clearly indicate that the development of small, abnormal dI1 in both jaws is the "normal" or usual condition during early dental ontogeny in the African rodent families Bathyergidae and Ctenodactylidae, and probably also in Anomaluridae and Pedetidae. These observations provide additional corroboration for the hypothesis (LUCKETT 1985) that the presence of rudimentary dI1 during fetal life characterized the last common ancestor of extant rodents.

The developmental pattern of the abnormal dI1 and their relationships with the large, normal dI2 in bathyergids and ctenodactylids are similar in most respects with the condition described previously for sciurids (LUCKETT 1985). In these groups, the rudimentary teeth develop to the bell stage, but differ from normal teeth in that stellate reticulum does not differentiate during this stage. Concomitant with this, there is a lack of ameloblasts and enamel in later stages. Although the reasons are not completely understood, stellate reticulum appears to be necessary for the normal development of enamel in mammals. Another abnormal feature of rodent dI1 is the formation of an irregular dentinal knot, in which the odontoblasts become partially entrapped within the dentin, rather than forming a distinct odontoblastic layer. These abnormal attributes of rodent dI1 also characterize the developmental pattern of abnormal or vestigial deciduous teeth in a variety of other mammals (MOSS-SALENTIJN 1978; LUCKETT and MAIER 1982; LUCKETT and ZELLER in press).

In contrast to the apparent consistent presence of small dI1 during early ontogeny in sciurids, bathyergids and ctenodactylids, they seem to be of more variable occurrence in muroid and caviomorph rodents. Thus, early studies (FREUND 1892; ADLOFF 1898) failed to detect rudimentary dI1 in *Mus*, except in a single fetus described by WOODWARD (1894). However, a later study on a closely graded developmental series indicated that a tiny dI1 may be a normal constituent of the upper jaw during fetal and early postnatal life in *Mus* (FITZGERALD 1973). MOSS-SALENTIJN (1978) has also reported the variable occurrence of rudimentary deciduous incisors in the rat. The distribution of these teeth in other muroids is unknown.

Despite numerous investigations of dental development in the South American caviomorph *Cavia* (FREUND 1892; ADLOFF 1898; TIMS 1901; HARMAN and SMITH 1936; BERKOVITZ 1972), there appears to be only a single report of a possible rudimentary

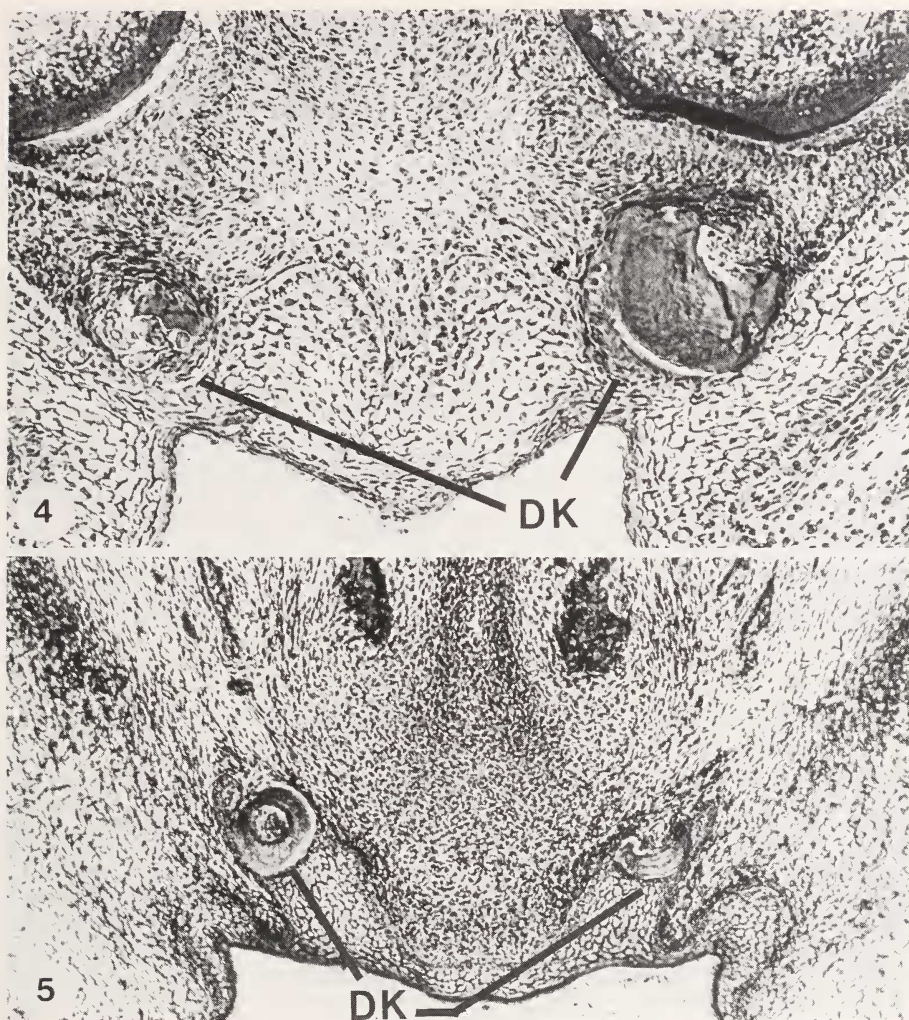


Fig. 4. *Ctenodactylus gundi* 41 mm CR fetus. Transverse section through upper jaw, showing the remnants of dI1 as tiny, partially resorbed, dentinal knots (DK). The tooth on the left side is almost completely resorbed. ($\times 450$). – Fig. 5. *Anomalurops beecrofti* 44 mm CR fetus. Transverse section through upper jaw, showing tiny, partially resorbed, dentinal knots (DK) of dI1 projecting into the oral epithelium. ($\times 250$)

deciduous incisor in this genus. ADLOFF (1898) believed that an early cap-like thickening in the lower jaw of a 30 mm head length (HL) fetus was homologous to the first deciduous incisor, although such a rudiment was absent in the upper jaw. In contrast, he found no trace of such a tooth in a younger 15 mm HL specimen, nor in a 40 mm HL *Dasyprocta* fetus. Until now, the only evidence for an unquestioned abnormal deciduous incisor in caviomorphs was the brief description and illustration of a tiny cap-like dentinal mass in both jaws of a single fetus of *Dactylomys* (family Echimyidae) by MULLER (1927). Recently, we have prepared serial sections through a fetal head of the caviid *Galea musteloides* (27 mm CR; 14 mm HL), from the collection of the Zoology Department,

University of Tübingen. It possesses a small, well developed cap-like dentinal rudiment for dl_1 in the lower jaw, whereas only a condensed mass of connective tissue indicates the possible remnant of dl^1 in the upper jaw. Additional developmental stages of other caviomorph families should be investigated in order to determine the distribution of abnormal incisors in Caviomorpha.

The widespread occurrence of abnormal $dl1$ during ontogeny in rodent families suggests that these tooth germs may play an important functional role, despite their abnormal and transitory nature. If this is true, their functional activity is probably limited to the early phases of dental development in the fetus. Further understanding of the developmental interrelationships between oral ectoderm and migrating neural crest cells during the initial stages of dental lamina and tooth bud formation (LUMSDEN 1984) should provide additional insight into the ontogenetic and phylogenetic significance of abnormal deciduous incisors in rodents.

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Zusammenfassung

Über das Auftreten abnormaler Incisiven im Milchgebiß während der pränatalen Entwicklung bei afrikanischen „hystricomorphen“ Rodentia

Frühe Stadien der Zahnentwicklung wurden in vier Familien und fünf Gattungen afrikanischer „hystricomorphen“ Nager untersucht. Kleine, abnormale vordere Milchzähne (Incisiven, $dl1$) wurden sowohl im Oberkiefer als auch im Unterkiefer beobachtet. Sie treten rostral der großen, normalen $dl2$ in frühen Entwicklungsstadien aller untersuchten Arten auf (*Bathyergus janetta*, *Georychus capensis*, *Ctenodactylus gundi*, *Pedetes caffer* und *Anomalurops beecrofti*). Die kleinen abnormalen Zähne entwickeln einen unregelmäßigen Dentinkern, weisen jedoch weder Ameloblasten noch Schmelz auf. Ein ähnliches morphogenetisches Erscheinungsbild bieten die vorderen Milchzähne der Sciuriden, und es entspricht wahrscheinlich dem für Nager ursprünglichen Zustand. Die funktionelle Bedeutung dieser abnormalen Zähne in der Ontogenese ist bis jetzt unbekannt.

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